Subterranean Biology 53: 129–153 (2025)
doi: 10.3897/subtbiol.53.163632
https://subtbiol.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

Terrestrial isopods (Crustacea, Isopoda, Oniscidea) from Mesovoid Shallow Substratum habitats of Portugal

Rita P. Eusébio[1], Stefano Taiti[2], Ana Sofia P. S. Reboleira[1,3]

1 *Centre for Ecology, Evolution and Environmental Changes (CE3C) and CHANGE – Global Change and Sustainability Institute, and Departamento de Biologia, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749–016, Lisboa, Portugal* **2** *Istituto di Ricerca sugli Ecosistemi Terrestri, Consiglio Nazionale delle Ricerche, Via Madonna del Piano 10, 50019 Sesto Fiorentino (Firenze), Italy* **3** *Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Rua da Escola Politécnica, Lisboa, Portugal*

Corresponding author: Ana Sofia P. S. Reboleir (asreboleira@fc.ul.pt)

Academic editor: Fabio Stoch | Received 30 June 2025 | Accepted 25 August 2025 | Published 8 October 2025

https://zoobank.org/98FAD49E-ED52-4C9E-82B5-120452E46F19

Citation: Eusébio RP, Taiti S, Reboleira ASPS (2025) Terrestrial isopods (Crustacea, Isopoda, Oniscidea) from Mesovoid Shallow Substratum habitats of Portugal. Subterranean Biology 53: 129–153. https://doi.org/10.3897/subtbiol.53.163632

Abstract

The Mesovoid Shallow Substratum (MSS) is a largely unknown subterranean habitat formed by the accumulation of rock fragments in steep slopes. In this study, we investigated the diversity, abundance and seasonal dynamics of terrestrial isopods in MSS habitats across Portugal. We identified 12 species belonging to five families, with Porcellionidae and Armadillidiidae being the most represented. The new species, *Eluma cristata*, endemic to the MSS of Alcobertas, is described. The terrestrial isopod communities included both surface-dwelling and subterranean-adapted species, pointing out the connectivity between these habitats and highlighting the adaptability of terrestrial isopods to diverse environments. Widespread species occurring in multiple locations, and species confined to single sites are present. Seasonality does not seem to affect the community composition. Our findings highlight the rich diversity of MSS habitats, thus their importance for conservation.

Keywords

Crustaceans, Iberian Peninsula, new species, shallow subterranean habitats, subterranean ecosystems

Copyright *Rita P. Eusébio et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Subterranean habitats are some of the least explored ecosystems in terms of biodiversity (Mammola et al. 2019, 2020). Among these, the Mesovoid Shallow Substratum (MSS), a network of voids formed by the accumulation of rock fragments in steep slopes, has received limited attention despite its ecological importance (Juberthie et al. 1980; Mammola et al. 2016).

While deep subterranean habitats such as caves have increasingly attracted scientific and public attention for their biodiversity and conservation value (Mammola et al. 2019), MSS habitats, despite their global distribution across varied geomorphological settings, remain poorly studied. Their faunal composition and ecological dynamics are still poorly understood (Eusébio et al. 2021).

MSS habitats are characterized by relatively stable microclimatic conditions, including reduced thermal fluctuations compared with surface habitats. These features provide both a refuge from surface climatic extremes and a permanent habitat for a diverse range of species (Nitzu et al. 2014; Mammola et al. 2016). These habitats support rich and specialized invertebrate communities, including both subterranean-adapted and surface-dwelling species (Culver and Pipan 2009, 2014; Mammola et al. 2016, 2017).

Terrestrial isopods frequently found in subterranean ecosystems have limited dispersal abilities and preference for high moisture (Hornung 2011; Dixie et al. 2015). Very few papers deal with terrestrial isopods from the MSS (e.g., Nitzu et al. 2010, 2011; Reboleira et al. 2015, 2022; Cifuentes et al. 2021). In Portugal, terrestrial isopod fauna of subterranean habitats has been documented in caves and sporadically in the MSS (Vandel 1946; Reboleira et al. 2015, 2022). However, comprehensive data on isopod diversity, distribution and seasonal dynamics in MSS habitats of Portugal are still lacking.

Subterranean habitats and their specialized fauna face increasing threats from land-use change, global warming, and pollution (Mammola et al. 2019; Reboleira and Eusébio 2021, 2023; Reboleira et al. 2022). While cave invertebrates have been increasingly included in conservation assessments such as the IUCN Red List (IUCN 2025) and the Portuguese Red Book of Invertebrates (ICNF 2023), species from shallow subterranean habitats remain overlooked, despite their vulnerability and ecological importance (Eusébio et al. 2021).

We studied the diversity, abundance, and seasonal dynamics of terrestrial isopods in MSS habitats in Portugal. We analysed new spatial-temporal distribution patterns and described a new species of the genus *Eluma* Budde-Lund, 1885. This information is crucial to underline the relevance of the conservation of these shallow subterranean ecosystems.

Material and methods

Terrestrial isopod sampling was conducted in five MSS areas across Portugal: Unhais da Serra, Serra da Estrela (40°17'23.7"N, 7°35'20.1"W) at 1.330 m a.s.l, Vale dos Poios, Sicó (39°58'49.3"N, 8°33'03.1"W) at 150 m, Alcobertas, Estremenho Karst Massif (39°25'46.8"N, 8°54'58.7"W) at 400 m, Cabanas de Torres, Montejunto

(39°10'11.2"N, 9°04'14.1"W) at 420 m, and São Lourenço, Arrábida (38°28'59.3"N, 9°00'09.9"W) at 300 m (Fig. 1).

Specimens were collected using pitfall traps modified to sample MSS habitats following the method of Eusébio et al. (2021), with only one collecting pitfall cup at a 50 cm depth. In each location five traps were installed, 10 m away from each other and 1 m away from the shrub edge, using pork liver as bait and propylene glycol as a preserving liquid. Samples were collected every three months for one year (March 2022 – March 2023).

Terrestrial isopod specimens were identified to species level based on morphological characters and the pertinent literature, under Wild M5 and M20 microscopes. Specimens were dissected and mounted in micro preparations using Hoyer's liquid.

Specimens were drawn using a camera lucida, and photographed using a Leica DMC4500 camera, with a Leica Z6 APO microscope, and stacked with the Leica LAS X software. Background of specimens' images was cleaned using Adobe Photoshop (Version 24.2.0).

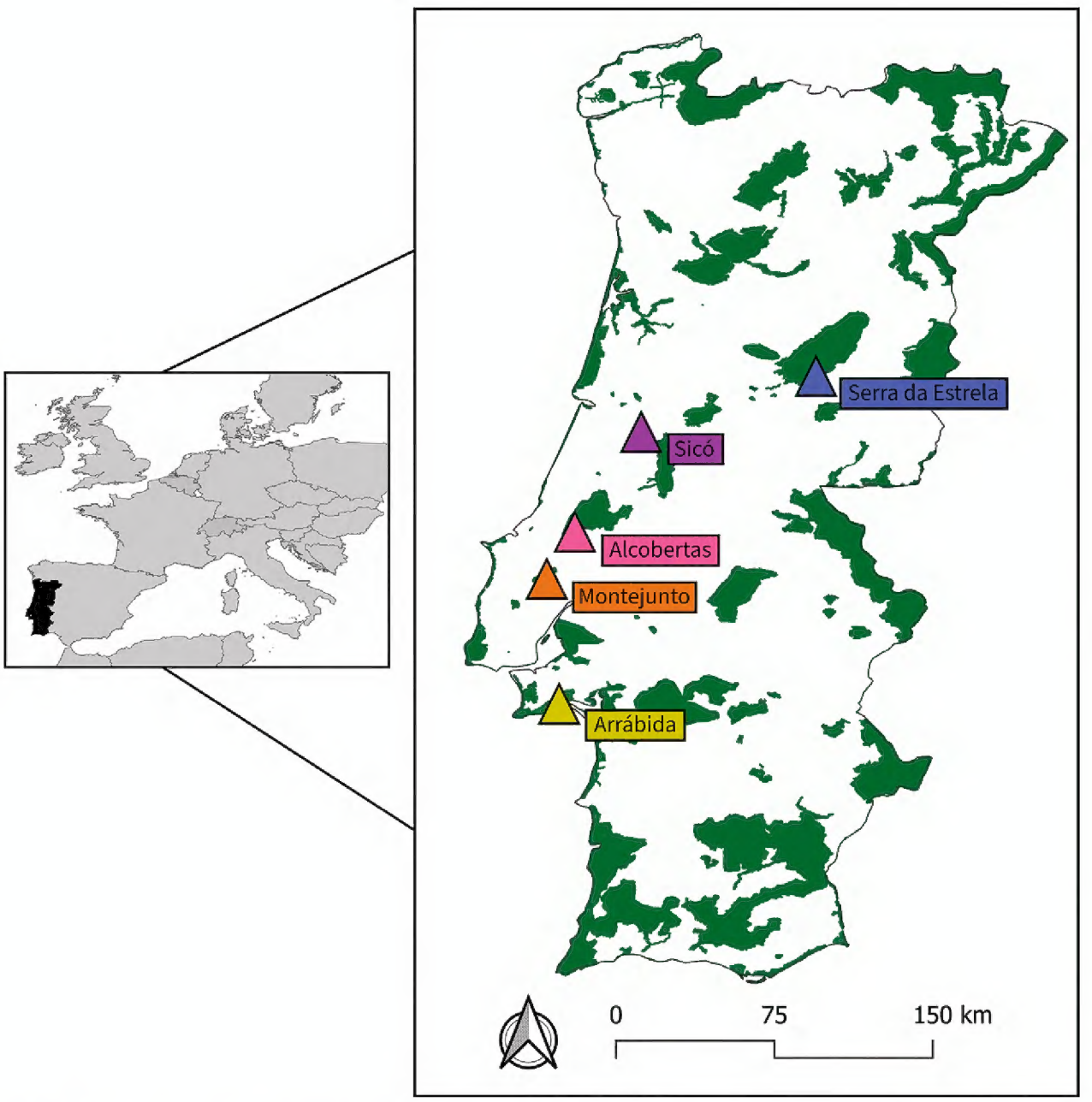

Figure 1. Distribution map. Sampling locations marked in coloured triangles: blue – Serra da Estrela, purple – Sicó, pink – Alcobertas, orange – Montejunto, yellow – Arrábida. The green zones represent the protected areas of Portugal.

Data analysis was done in R software version 4.4.2 (R Core Team 2024). Species abundance was visualized using the ggplot function (Wickham 2016). Non-metric multidimensional scaling (NMDS) was used to visualize the spatial and seasonal community patterns, using the Bray-Curtis dissimilarity in the vegan package (Oksanen et al. 2025), only considering stress values below 0.2, which indicate a good data representation of the two-dimensional ordination space (Clarke 1993).

Specimens are deposited in the National Museum of Natural History and Science (**MNHNC**), in the crustacean collection (**MB11**), University of Lisbon, Portugal, and in the Museo di Storia Naturale "La Specola" (**MZUF**), Florence, Italy.

Results

Taxonomy

Class Malacostraca Latreille, 1802
Order Isopoda Latreille, 1817
Suborder Oniscidea Latreille, 1802
Family Trichoniscidae Sars, 1899
Genus *Trichoniscoides* Sars, 1899

***Trichoniscoides machadoi* Vandel, 1946**
Fig. 6A

Trichoniscoides machadoi Vandel, 1946: 168, figs 8–12; Vandel 1947: 270; Vandel 1948: 129, fig. 14;Vandel 1952: 262, figs 2, 9; Schmölzer 1965: 37, figs 79–82; Schmölzer 1971: 4, 75, 139, map 4; Schmalfuss 2003: 303; Reboleira et al. 2015: 6, fig. 2; Cifuentes 2019: 48; Cifuentes and Da Silva 2023: 7.

Material examined. Portugal – **Sicó** • 2 ♂♂, 3 ♀♀; 39°58'51.8"N, 8°33'13.1"W; 19.XII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001283, 001285, 001287 • 1 ♀; 20.III.2023; same data as for preceding; MNHNC:MB11:001379. – **Arrábida** • 1 ♂, 2 ♀♀; 38°28'59.2"N, 9°00'09.9"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001141 • 3 ♂♂; 22.III.2023; same data as for preceding; MNHNC:MB11:001313, 001323.

Distribution. Endemic to Portugal. This species is widely distributed throughout the country.

Ecological notes. This species can be found in caves, MSS, and endogean habitats.

Seasonal patterns in Portuguese MSS habitats. This species was found in two locations, Sicó and Arrábida. In Sicó it was captured during fall and winter, with a higher abundance in fall (Fig. 7A). In Arrábida it was captured during spring and fall in equal abundances (Fig. 7A).

Family Philosciidae Kinahan, 1857
Genus *Ctenoscia* Verhoeff, 1928

Ctenoscia minima (Dollfus, 1892)
Fig. 6B

Philoscia minima Dollfus, 1892: 187, fig. 3.
Philoscia (*Benthana*) *minima* Jackson, 1926: 196, pl. VIII figs 152–165.
Ctenoscia minima Vandel, 1946: 196, figs 42–49; Schmölzer 1965: 141, fig. 605; Schmölzer 1971: 20; Schmalfuss 2003: 87; Reboleira et al. 2015: 40; Cifuentes and Da Silva 2023: 36.
Ctenoscia dorsalis; Gregory et al. 2012: 17.

Material examined. Portugal – **Sicó** • 19 ♀♀; 39°58'51.8"N, 8°33'13.1"W; 20.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001130, 001133, 001144, 001149, 001165 • 1 ♀; 19.IX.2022; same data as for preceding; MNHNC:MB11:001256. – **Alcobertas** • 1 ♂, 3 ♀♀; 39°25'46.5"N, 8°54'59.0"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001185, 001187, 001202 • 6 ♀♀; 20.IX.2022; same data as for preceding; MNHNC:MB11:001205, 001212, 001218 • 3 ♀♀; 20.XII.2022; same data as for preceding; MNHNC:MB11:001294, 001298 • 1 ♂, 2 ♀♀; 01.IV.2023; same data as for preceding; MNHNC:MB11:001357, 001360. – **Montejunto** • 2 ♂♂, 13 ♀♀; 39°10'11.4"N, 9°04'14.8"W; 22.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001181, 001192 • 2 ♂♂, 3 ♀♀; 21.IX.2022; same data as for preceding; MNHNC:MB11:001223, 001231 • 2 ♂♂; 21.XII.2022; same data as for preceding; MNHNC:MB11:001340 • 2 ♀♀; 21.III.2023; same data as for preceding; MNHNC:MB11:001385. – **Arrábida** • 17 ♀♀, 1 juv.; 38°28'59.2"N, 9°00'09.9"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001137, 001151, 001154, 001172, 001176 • 4 ♂♂, 10 ♀♀, 2 juvs; 20.IX.2022; same data as for preceding; MNHNC:MB11:001233, 001237, 001245 • 2 ♂♂, 11 ♀♀; 20.XII.2022; same data as for preceding; MNHNC:MB11:001306, 001314, 001324.

Distribution. Portugal, Spain, Italy, France (Corsica), Malta, Tunisia, and Morocco.

Ecological notes. This epigean species can also be found in caves and MSS.

Seasonal patterns in Portuguese MSS habitats. This species was found in four locations, Sicó, Alcobertas, Montejunto and Arrábida. In Sicó it was captured during spring and summer, with a higher abundance in spring (Fig. 7B). In Alcobertas it was captured during all seasons, with abundance increasing towards summer and then decreasing till winter (Fig. 7B). In Montejunto this species was also captured during all seasons, with abundance decreasing steadily towards fall and then staying the same in winter (Fig. 7B). In Arrábida it was captured during spring, summer, and fall, with a steady decrease in abundance from spring to fall (Fig. 7B).

Family Porcellionidae Brandt, 1831
Genus *Porcellionides* Miers, 1877

Porcellionides cingendus (Kinahan, 1857)
Fig. 6C

Porcellio cingendus Kinahan, 1857: 279, figs. 1, 2, 4, 6, 8, 9.
Porcellio (*Porcellionides*) *lusitanorum* Arcangeli, 1935a: 21, figs 13–18.
Metoponorthus (*Lusitoniscus*) *cingendus* Vandel, 1946: 274, figs 91–97; Schmölzer 1965: 195, figs 698–699; Schmölzer 1971: 33.
Porcellionides cingendus Schmalfuss, 2003: 240; Gregory et al. 2012: 18; Reboleira et al. 2015; Cifuentes and Da Silva 2024: 4, figs 1, 2A, 3A, 4A–D, 5, tab. 1.

Material examined. Portugal – **Sicó** • 54 ♂♂, 58 ♀♀, 2 juvs; 39°58'51.8"N, 8°33'13.1"W;20.VII.2022;leg.R.P.Eusébio;MSSpitfalltrap;MNHNC:MB11:001123, 001127, 001128, 001129, 001134, 001143, 001147, 001166 • 18 ♂♂, 38 ♀♀; 19.IX.2022; same data as for preceding; MNHNC:MB11:001255, 001257, 001258, 001259, 001262, 001263 • 32 ♂♂, 31 ♀♀; 19.XII.2022; same data as for preceding; MNHNC:MB11:001275, 001278, 001282, 001284, 001288 • 30 ♂♂, 6 ♀♀; 20.III.2023; same data as for preceding; MNHNC:MB11:001372, 001374, 001376, 001381, 001383. – **Alcobertas** • 6 ♂♂, 21 ♀♀; 39°25'46.5"N, 8°54'59.0"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001188, 001197, 001199, 001201 • 13 ♂♂, 58 ♀♀; 20.IX.2022; same data as for precedings; MNHNC:MB11:001204, 001211, 001215, 001217 • 34 ♂♂, 46 ♀♀; 20.XII.2022; same data as for preceding; MNHNC:MB11:001293, 001297, 001299, 001303 • 56 ♂♂, 23 ♀♀; 01.IV.2023; same data as for preceding; MNHNC:MB11:001350, 001352, 001353, 001358. – **Montejunto** • 32 ♂♂, 44 ♀♀; 39°10'11.4"N, 9°04'14.8"W; 23.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001161, 001178, 001180, 001190 • 3 ♂♂, 33 ♀♀; 21.IX.2022; same data as for preceding; MNHNC:MB11:001220, 001222, 001226, 001230 • 55 ♂♂, 57 ♀♀, 2 juvs; 21.XII.2022; same data as for preceding; MNHNC:MB11:001329, 001338, 001339, 001346 • over 500 specimens (♂ and ♀); 21.III.2023; same data as for preceding; MNHNC:MB11:001387, 001393, 001397, 001400, 001403. – **Arrábida** • 11 ♂♂, 17 ♀♀, 3 juvs; 38°28'59.2"N, 9°00'09.9"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001136, 001142, 001155, 001171, 001175 • 18 ♂♂, 64 ♀♀, 46 juvs; 20.IX.2022; same data as for preceding; MNHNC:MB11:001234, 001236, 001242, 001246 • over 200 specimens (♂ and ♀); 20.XII.2022; same data as for preceding; MNHNC:MB11:001307, 001315, 001320, 001325, 001332 • 2 ♂♂, 2 ♀♀, 1 juv.; 22.III.2023; same data as for preceding; MNHNC:MB11:001363, 001368.

Distribution. United Kingdom, France and Iberian Peninsula.

Ecological notes. This epigean species can also occur in caves and MSS.

Seasonal patterns in Portuguese MSS habitats. This species was found in four locations, Sicó, Alcobertas, Montejunto and Arrábida. Specimens were found during all seasons in the four locations. In Sicó there was a steady decrease in abundance from spring to winter, in Alcobertas there was an increase from spring to winter, in Montejunto abundance decreased from spring to summer and then increased until winter (Fig. 7C). In Arrábida abundance increased steadily until fall and then decreased to exceptionally low numbers in winter (Fig. 7C).

Genus *Porcellio* Latreille, 1804

Porcellio scaber Latreille, 1804

Fig. 6D

Porcellio scaber Latreille, 1804: 45; Dollfus 1897: 206; Vandel 1946: 297; Gregory et al. 2012: 20, fig. 6.
Porcellio (*Porcellio*) *scaber* Arcangeli, 1935a: 9.
Porcellio (*Euporcellio*) *scaber* var. *scabrior* Verhoeff, 1907: 266.
Porcellio scaber scaber Schmölzer, 1971: 39.

Material examined. Portugal – **Serra de Estrela** • 1 ♂, 1 ♀; 40°17'22.9"N, 7°35'19.7"W; 20.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001167 • 1 ♂, 9 ♀♀; 19.IX.2022; same data as for preceding; MNHNC:MB11:001240, 001248, 001249 • 1 ♂, 1 ♀; 19.XII.2022; same data as for preceding; MNHNC:MB11:001269, 001273.

Distribution. Widespread in Europe and introduced into many parts of the world.

Ecological notes. This epigean species can also be found in MSS.

Seasonal patterns in Portuguese MSS habitats. This species was found in one location, Serra da Estrela, during spring, summer, and fall, and with abundance peaking in summer (Fig. 7D).

Porcellio dilatatus Brandt, 1831

Fig. 6E

Porcellio dilatatus Brandt in Brandt and Ratzeburg 1831: 78, Pl. 12, fig. 6c, d; Vandel 1946: 316, fig. 135; Schmölzer 1971: 44.
Porcellio (*Porcellio*) *dilatatus* Arcangeli, 1935a: 12.
Porcellio dilatatus dilatatus; Reboleira et al. 2015: 46.

Material examined. Portugal – **Sicó** • 1 ♀; 39°58'51.8"N, 8°33'13.1"W; 20.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001122 • 1 ♂; 19.XII.2022; same data as for preceding; MNHNC:MB11:001274 • 1 ♂, 3 ♀♀; 20.III.2023; same data as for preceding; MNHNC:MB11:001371, 001382. – **Montejunto** • 1 ♂; 39°10'11.4"N,

9°04'14.8"W; 21.III.2023; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001389. – **Arrábida** • 22 ♂♂, 41 ♀♀, 182 juvs; 38°28'59.2"N, 9°00'09.9"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001135, 001138, 001140, 001150, 001152, 001158, 001169, 001170, 001173, 001174 • 2 ♂♂, 12 ♀♀, 20 juvs; 20.IX.2022; same data as for preceding; MNHNC:MB11:001235, 001238, 001243, 001247 • 28 ♂♂, 23 ♀♀, 32 juvs; 20.XII.2022; same data as for preceding; MNHNC:MB11:001304, 001308, 001310, 001316, 001317, 001319, 001322, 001326, 001330, 001333 • 16 ♂♂, 13 ♀♀; 22.III.2023; same data as for preceding; MNHNC:MB11:001361, 001364, 001365, 001366.

Distribution. Common across Europe and introduced into many parts of the world.

Ecological notes. This species is mainly found in caves and MSS habitats but does not show any adaptation to subterranean habitats.

Seasonal patterns in Portuguese MSS habitats. This species was found in three locations, Sicó, Montejunto and Arrábida. In Sicó and Montejunto it was found in very low numbers (Fig. 7E). In Arrábida it was captured during all seasons, with abundance decreasing from spring to summer, then increasing slightly in fall and decreasing again in winter (Fig. 7E).

Porcellio dispar Verhoeff, 1901

Fig. 6F

Porcellio dispar Verhoeff, 1901: 407; Vandel 1946: 289, figs 110–111; Schmölzer 1965: 228; Schmölzer 1971: 36; Schmalfuss, 2003: 222; Cifuentes and Da Silva 2023: 36.
Porcellio (*Euporcellio*) *dispar* Verhoeff, 1907: 269.
Porcellionides dimorphus Jackson, 1926: 186, pl. I figs 1–22.
Porcellio (*Porcellio*) *dispar* Arcangeli, 1935a: 10, figs 3–7.

Material examined. Portugal – **Sicó** • 6 ♀♀; 39°58'51.8"N, 8°33'13.1"W; 20.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001131, 001145, 001164 • 1 ♀; 19.IX.2022; same data as for preceding; MNHNC:MB11:001264 • 2 ♀♀; 19.XII.2022; same data as for preceding; MNHNC:MB11:001277 • 3 ♀♀; 20.III.2023; same data as for preceding; MNHNC:MB11:001373. – **Montejunto** • 2 ♂♂, 4 ♀♀; 39°10'11.4"N, 9°04'14.8"W; 23.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001160, 001179 • 1 ♀; 21.XII.2022; same data as for preceding; MNHNC:MB11:001343 • 3 ♂♂, 23 ♀♀; 21.III.2023; same data as for preceding; MNHNC:MB11:001386, 001394.

Distribution. Portugal, NW Spain, and France.

Ecological notes. This epigean species can also be found in caves and MSS.

Seasonal patterns in Portuguese MSS habitats. This species was found in two locations, Sicó and Montejunto. In Sicó it was captured in all seasons, with abundance decreasing from spring to summer, then increasing slightly until winter (Fig. 7F). In Montejunto it was captured during spring, fall and winter, with abundance decreasing from spring to fall and increasing to its highest in winter (Fig. 7F).

***Porcellio novus* Arcangeli, 1935**
Fig. 6G

Porcellio (*Porcellio*) *novus* Arcangeli, 1935b: 40, figs 1–6.
Porcellio novus Vandel, 1946: 322; Schmölzer 1955: 314; Schmölzer 1965: 230, fig. 835; Schmölzer 1971: 38; Schmalfuss, 2003: 231.

Material examined. Portugal – Alcobertas • 2♂♂, 3♀♀; 39°25'46.5"N, 8°54'59.0"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001196 • 6 ♂♂, 10 ♀♀, 1juv.; 20.IX.2022; same data as for preceding; MNHNC:MB11:001208, 001210, 001214, 001219 • 1 ♂, 3 ♀♀; 20.XII.2022; same data as for preceding; MNHNC:MB11:001290, 001292 • 2 ♀♀; 1.IV.2023; same data as for preceding; MNHNC:MB11:001355.

Distribution. Portugal and western Spain.

Ecological notes. This epigean species can also be found in MSS.

Seasonal patterns in Portuguese MSS habitats. This species was found in one location, Alcobertas, during all seasons, with abundance increasing from spring to summer, then decreasing steadily towards winter (Fig. 7G).

Family Armadillidiidae Brandt, 1833

Genus *Eluma* Budde-Lund, 1885

***Eluma caelata* (Miers, 1877)**
Fig. 6H

Armadillidium caelatum Miers, 1877: 665, pl. 7 fig. 3.
Rhacodes inscriptus Eaton, 1882: 360 (not *Rhacodes inscriptus* C.L. Koch in Rosenhauer 1856: 422).
Eluma purpurascens Budde-Lund, 1885: 48, 294; Preudhomme de Borre 1886: 112; Dollfus 1889a: 126; Dollfus 1889b: 306; Dollfus 1896a: 357; Norman 1899: 69; Verhoeff 1908: 370; Vandel 1946: 357, fig. 158.
Eluma caelatum Arcangeli, 1935a: 3; Arcangeli 1948: 242; Schmölzer 1965: 303, fig. 1213; Schmölzer 1971: 58; Schmalfuss 2003: 107.
Eluma caelata Gregory et al., 2012: 21, tab. 2, 3; Reboleira et al. 2015: 47; Recuero et al. 2022: 1315, tab. 1; Cifuentes and Da Silva 2023: 29, figs 1A, 2A-C, 4G.

Material examined. Portugal – Serra de Estrela • 1 ♀; 40°17'22.9"N, 7°35'19.7"W; 20.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001121 • 1 ♂, 1 ♀; 19.IX.2022; same data as for preceding; MNHNC:MB11:001250 • 5 ♂♂, 7 ♀♀; 19.XII.2022; same data as for preceding; MNHNC:MB11:001268, 001270, 001271, 001272 • 4 ♂♂, 5 ♀♀; 19.XII.2022; same data as for preceding; MZUF 10034 • 1 ♀; 20.III.2023; same data as for preceding; MNHNC:MB11:001347. – **Sicó** • 3 ♀♀; 39°58'51.8"N, 8°33'13.1"W; 20.VII.2022; leg. R.P. Eusébio;

MSS pitfall trap; MNHNC:MB11:001126, 001148, 001163 • 2 ♂♂, 3 ♀♀; 19.IX.2022; same data as for preceding; MNHNC:MB11:001251, 001254, 001265, 001267 • 1 ♀; 19.XII.2022; same data as for preceding; MNHNC:MB11:001280 • 3 ♀♀; 20.III.2023; same data as for preceding; MNHNC:MB11:001369, 001380. – **Alcobertas** • 34 ♂♂, 27 ♀♀; 39°25'46.5"N, 8°54'59.0"W; 1.IV.2023; leg. R.P. EusébioEusébio, R.P. leg; MSS pitfall trap; MNHNC:MB11:001349, 001359. – **Montejunto** • 14 ♂♂, 9 ♀♀; 39°10'11.4"N, 9°04'14.8"W; 23.VII.2022; ; MSS pitfall trap; MNHNC:MB11:001159, 001182, 001183, 001193 • 1 ♂, 11 ♀♀; 21.IX.2022; same data as for preceding; MNHNC:MB11:001221, 001224, 001228 • 11 ♂♂, 4 ♀♀; 21.XII.2022; same data as for preceding; MNHNC:MB11:001327, 001336, 001342, 001345 • 38 ♂♂, 26 ♀♀, 1 juv.; 21.III.2023; same data as for preceding; MNHNC:MB11:001388, 001391, 001395, 001398, 001401. – **Arrábida** • 8 ♂♂, 9 ♀♀; 38°28'59.2"N, 9°00'09.9"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001157 • 1 ♀; 20.XII.2022; same data as for preceding; MNHNC:MB11:001311 • 1 ♂, 2 ♀♀; 22.III.2023; same data as for preceding; MNHNC:MB11:001367.

Distribution. United Kingdom, France, Iberian Peninsula, The Netherlands, Belgium, Morocco, and Western Sahara. It was introduced to Australia (Tasmania) and French Guiana.

Ecological notes. This epigean species can also be found in caves and MSS.

Seasonal patterns in Portuguese MSS habitats. This species was found in all locations. In Serra da Estrela, Sicó and Montejunto it was captured during all seasons. In Serra da Estrela abundance increases towards fall then decreases in winter (Fig. 7H). In Sicó abundance increases toward summer, decreases in fall and increases again in winter (Fig.7H). In Montejunto abundance decreases in summer then increases steadily towards winter (Fig. 7H). In Alcobertas it was captured only in winter (Fig. 7H). In Arrábida it was captured during spring, fall and winter, with abundance decreasing from its peak in spring towards fall, then increasing slightly in winter (Fig. 7H).

Eluma tuberculata Cruz, 1991

Fig. 6I

Eluma tuberculata Cruz, 1991: 73, fig. 1a–f; Schmalfuss 2003:107; Reboleira et al. 2015: 49, figs 30, 31 (nec specimens from MSS near Gruta de Alcobertas, Estremenho Massif); Cifuentes and Da Silva 2023: 33, figs 1C, 2D-F, 4H.

Material examined. Portugal – **Sicó** • 68 ♂♂, 114 ♀♀; 39°58'51.8"N, 8°33'13.1"W; 20.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001124, 001125, 001132, 001146, 001162 • 5 ♂♂, 5 ♀♀; 20.VII.2022; same data as for preceding; MZUF 10035 • 39 ♂♂, 93 ♀♀, 13 juvs; 19.IX.2022; same data as for pre-

ceding; MNHNC:MB11:001252, 001253, 001260, 001261, 001266 • 10 ♂♂, 10 ♀♀; 19.IX.2022; same data as for preceding; MZUF 10036 • 27 ♂♂, 78 ♀♀, 14 juvs; 19.XII.2022; same data as for preceding; MNHNC:MB11:001276, 001279, 001281, 001286, 001289 • 23 ♂♂, 35 ♀♀; 20.III.2023; same data as for preceding; MNHNC:MB11:001370, 001375, 001377, 001378, 001384.

Distribution. Endemic to Portugal.

Ecological notes. This species can be found in caves and MSS habitats.

Seasonal patterns in Portuguese MSS habitats. This species was only found in Sicó, during all seasons, and with a decrease in abundance from spring to winter (Fig. 7I).

Eluma matae Cifuentes and Da Silva, 2023

Fig. 6J

Eluma matae Cifuentes & Da Silva, 2023: 33, figs 1B, 3, 4A-F, I, K-Q.

Material examined. **Portugal** – **Montejunto** • 6 ♂♂, 10 ♀♀; 39°10'11.4"N, 9°04'14.8"W; 22.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001177, 001184, 001194) • 10 ♀♀, 6 juvs; 21.IX.2022; same data as for preceding; MNHNC:MB11:001225, 001227, 001229 • 9 ♂♂, 13 ♀♀; 21.XII.2022; same data as for preceding; MNHNC:MB11:001328, 001335, 001337, 001344 • 5 ♂♂, 5 ♀♀; 21.XII.2022; same data as for preceding; MZUF 10037 • 30 ♂♂, 44 ♀♀, 1 juv.; 21.III.2023; same data as for preceding; MNHNC:MB11:001390, 001392, 001396, 001399, 001402.

Distribution. Endemic to Portugal.

Ecological notes. This epigean species can also be found in MSS.

Seasonal patterns in Portuguese MSS habitats. This species was only found in Montejunto, during all seasons, and with an increase in abundance from spring to winter (Fig. 7J).

Eluma cristata sp. nov.

https://zoobank.org/A53CD3DA-349D-4F64-BA23-DA0FD35C00D3

Figs 2–5, 6K

Eluma tuberculata Reboleira et al., 2015: 49 (partim: specimens from MSS near Gruta de Alcobertas, Estremenho Karst Massif).

Type material. ***Holotype.*** **Portugal** • ♂; **Alcobertas**; 39°25'46.5"N, 8°54'59.0"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001198. **Paratypes:** **Portugal** • 137 ♂♂, 138 ♀♀; same data as holotype; MNHNC:MB11:001186, 001189, 001195, 001198, 001200 • 115 ♂♂, 121 ♀♀; 20.IX.2022; same data as for

preceding; MNHNC:MB11:001203, 001207, 001209, 001213, 001216 • 5 ♂♂, 10 ♀♀; same data as for preceding; MZUF 10038 • 280 ♂♂, 240 ♀♀; 20.XII.2022; same data as for preceding; MNHNC:MB11:001291, 001295, 001296, 001301, 001302 • 10 ♂♂, 10 ♀♀; same data as for preceding; MZUF 10039 • 68 ♂♂, 103 ♀♀; 1.IV.2023; same data as for preceding; MNHNC:MB11:001348, 001351, 001354, 001356.

Description. Maximum length: ♂ 7.5 mm; ♀ 9.5 mm. Body strongly convex, able to roll up into perfect ball, euspheric type. Colour light brown, as in *E. matae* and *E. tuberculata*. Dorsal surface with ornamentation consisting of protruding crests on posterior margins of cephalon, pereonites 1–7 tergites and median part of pleonites 1–5, each crest ending in lobes of irregular shape and number; telson with two small paramedian tubercles (Figs 2A–E, 3A, G, H, 6K). Dorsum with scattered pointed scale-setae (Fig. 3B) and one line of noduli laterales per side located near top of crests on pereonites 1–7 far from lateral margins (Fig. 3G). Cephalon (Figs 2A–D, 3A, 6K) with triangular scutellum distinctly separated from and not bent over vertex; distinct frontal line and no postscutellar line; oblique antennary lobes, quadrangular and directed frontwards. Eye consisting of single large ocellus as in Fig. 2A,C. Pereonite 1 (Figs 2A, C, 3C, D, 6K) with deep dorsal groove on lateral margin, schisma on posterior corners with rounded inner lobe distinctly shorter than outer lobe; posterior margin slightly concave at sides. Pereonites 2 and 3 (Fig. 3E, F) epimera quadrangular with small and rounded lobe on ventral side. Pereonites 4–7 with quadrangular epimera and straight posterior margins. Pleonites 3–5 (Fig. 3G) with rectangular epimera, slightly divergent. Telson (Fig. 3G, H) triangular, wider than long, with slightly concave sides and rounded apex. Antennula (Fig. 3I) of three articles, second article much shorter than first and third, third article with tuft of superimposed aesthetascs subapically. Antenna (Fig. 4A) with flagellum slightly shorter than fifth article of peduncle, second flagellar article more than twice as long as first, bearing two aesthetascs on middle part. Mandibles (Fig. 4B, C) with dichotomized molar penicil and three or four free penicils; right mandible with one penicil and left mandible with two penicils on hairy lobe. Maxillula (Fig. 4D) outer lobe with 4 +6 (5 cleft) teeth; inner lobe with two thick subapical penicils and small triangular distal point. Maxilla (Fig. 4E) apically setose with outer lobe rounded, much wider than inner lobe. Maxilliped (Fig. 4F) with quadrangular endite bearing two triangular spines on distal margin and large subapical seta; basal article of palp with two large setae. Uropod (Fig. 4G) flattened; exopod about twice as wide as long with slightly concave distal margin; endopod slightly protruding backwards compared with exopod.

Male. Pereopod 1–3 (Fig. 5A) with line of pointed setae on sternal margins of carpus and, to lesser extent, merus. Pereopod 7 (Fig. 5B) ischium with sternal margin distinctly concave, distal margin with rounded lobe and four stout setae; merus with sternal margin slightly convex; merus and carpus with line of long setae on sternal margin. Genital papilla (Fig. 5C) fusiform. Pleopod 1 (Fig. 5C) exopod with large distal lobe bent outwards and apically rounded; endopod with distal part quadrangular

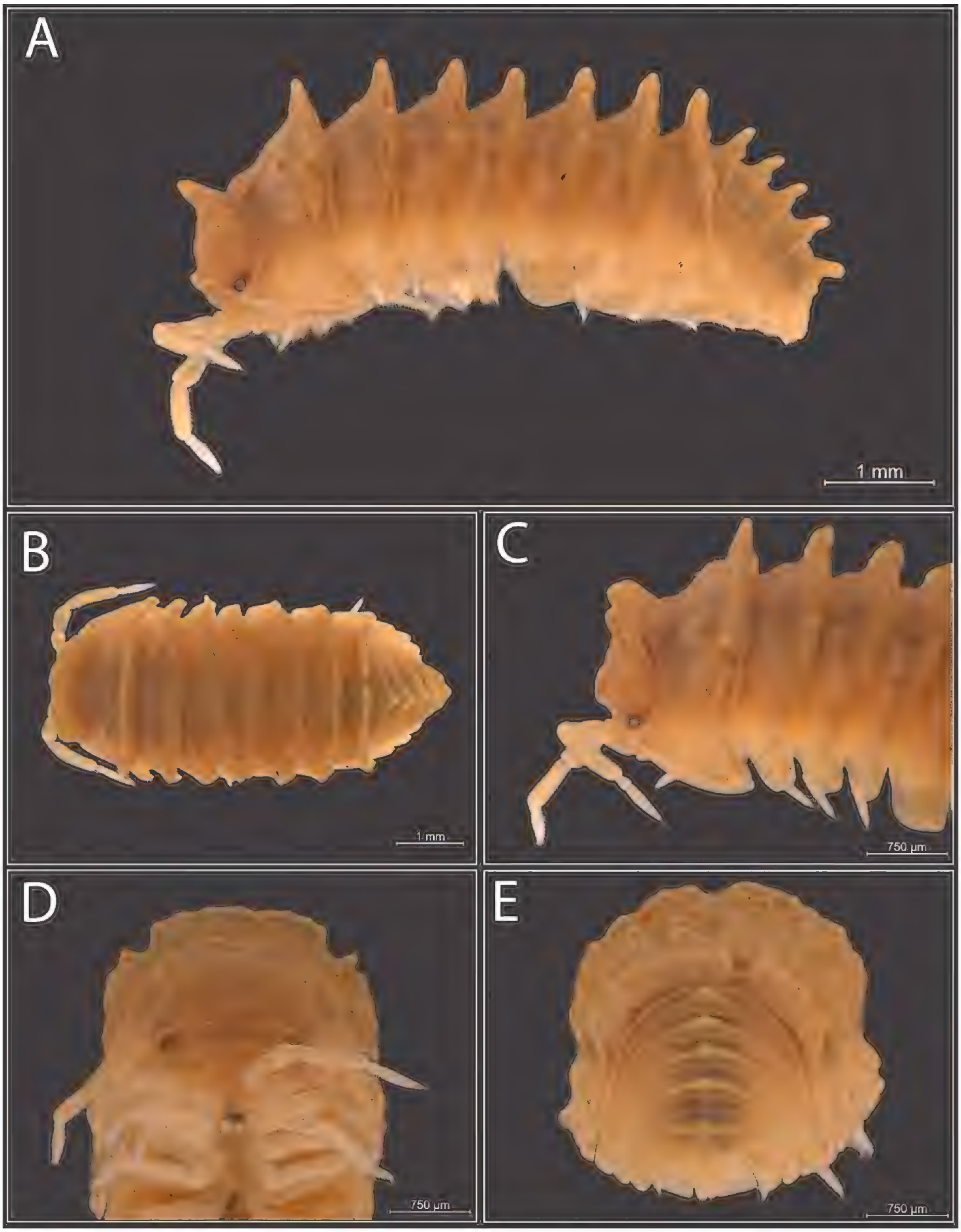

Figure 2. *Eluma cristata* sp. nov. Paratype ♂ from Alcobertas **A** adult specimen in lateral view **B** dorsal view **C** side view of the cephalon and pereonites 1–4 **D** frontal view of cephalon **E** dorsal view of posterior pereonites, pleon, telson and uropods.

and short apical lobe directed outwards. Pleopod 2 (Fig. 5D) exopod triangular with a line of about five short setae on outer margin; endopod slightly longer than exopod. Pleopods 3–5 exopods as in Fig. 5E–G.

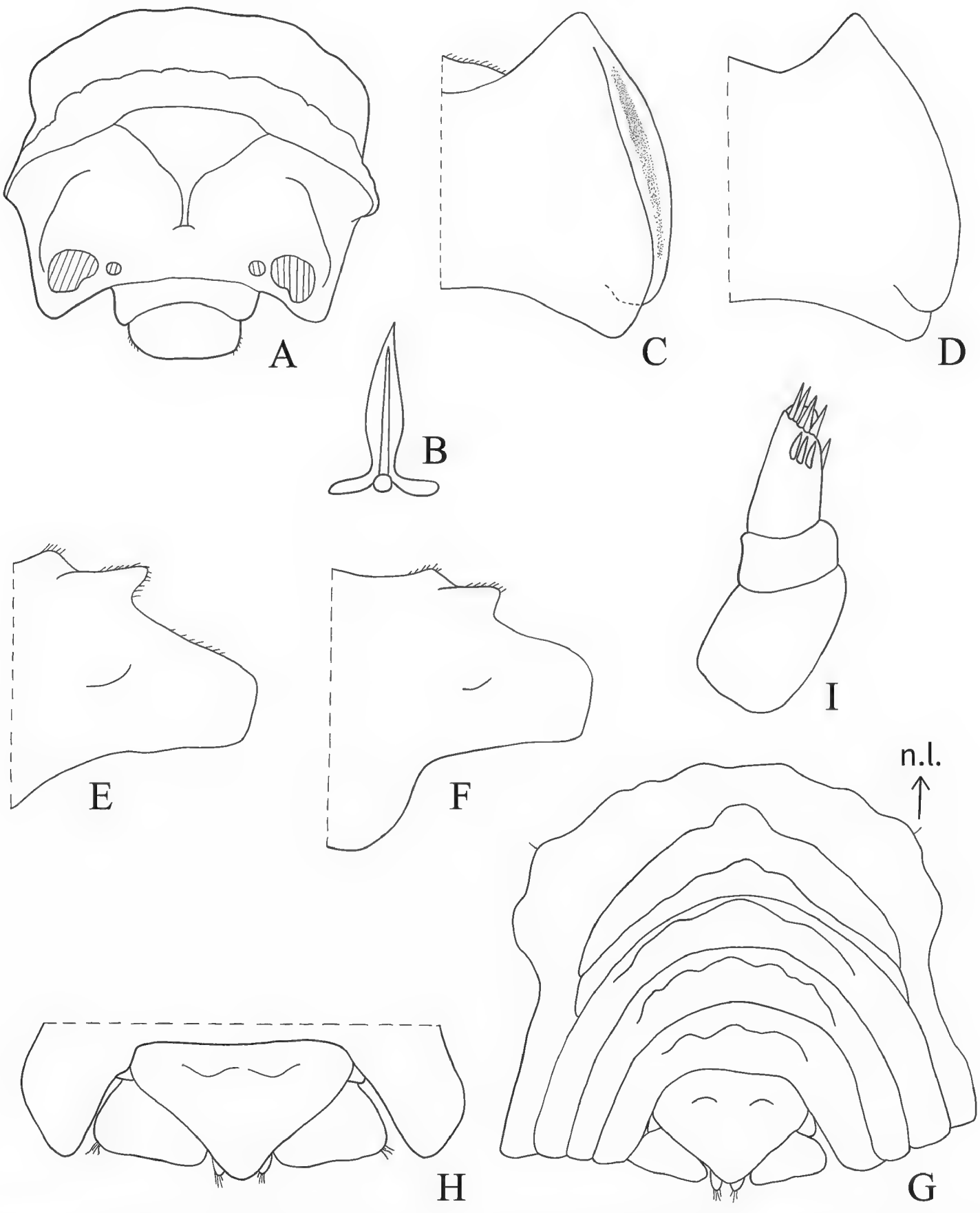

Figure 3. *Eluma cristata* sp. nov. Paratype ♂ from Alcobertas **A** cephalon, frontal **B** dorsal scale-seta **C** epimeron of pereonite 1, dorsal **D** epimeron of pereonite 1, ventral **E** epimeron of pereonite 2, ventral **F** epimeron of pereonite 3, ventral **G** pereonite 7, pleon, telson and uropods. n.l. = nodulus lateralis **H** telson and uropods **I** Antennula.

Etymology. From Latin *cristatus* = crested. The name refers to the high crests on the posterior margins of the body segments.

Remarks. At present, the genus *Eluma* comprises only five species, i.e., the four species included here and *E. praticola* Taiti & Rossano, 2015 from northern Morocco (see Schmalfuss 2003; Taiti and Rossano 2015; Cifuentes and Da Silva 2023).

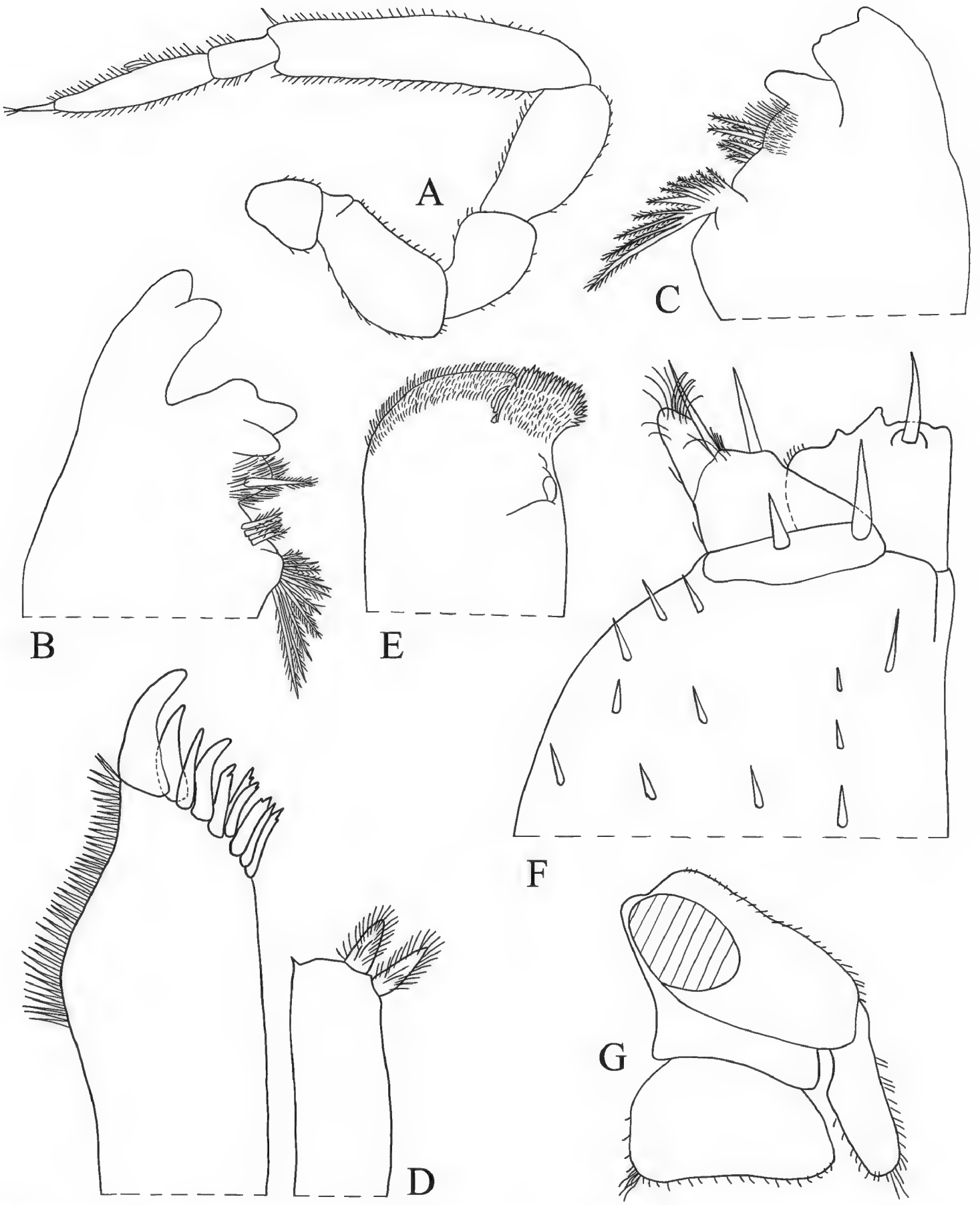

Figure 4. *Eluma cristata* sp. nov. Paratype ♂ from Alcobertas **A** antenna **B** right mandible **C** left mandible **D** maxillula **E** maxilla **F** maxilliped **G** uropod.

Eluma cristata sp. nov. is readily distinct from all the other species by the protruding dorsal crests on the posterior margins of the cephalon, pereonites and, to a lesser extent, pleonites. Moreover, it differs from *E. caelata* in lacking the basal triangular lobe on the male pereopod 7 merus (see fig. 32F,G in Taiti and Rossano 2015); from this species and *E. praticola* also in the male pleopod 1 endopod with thickset distal part, not bent outwards; from *E. matae* also in the much

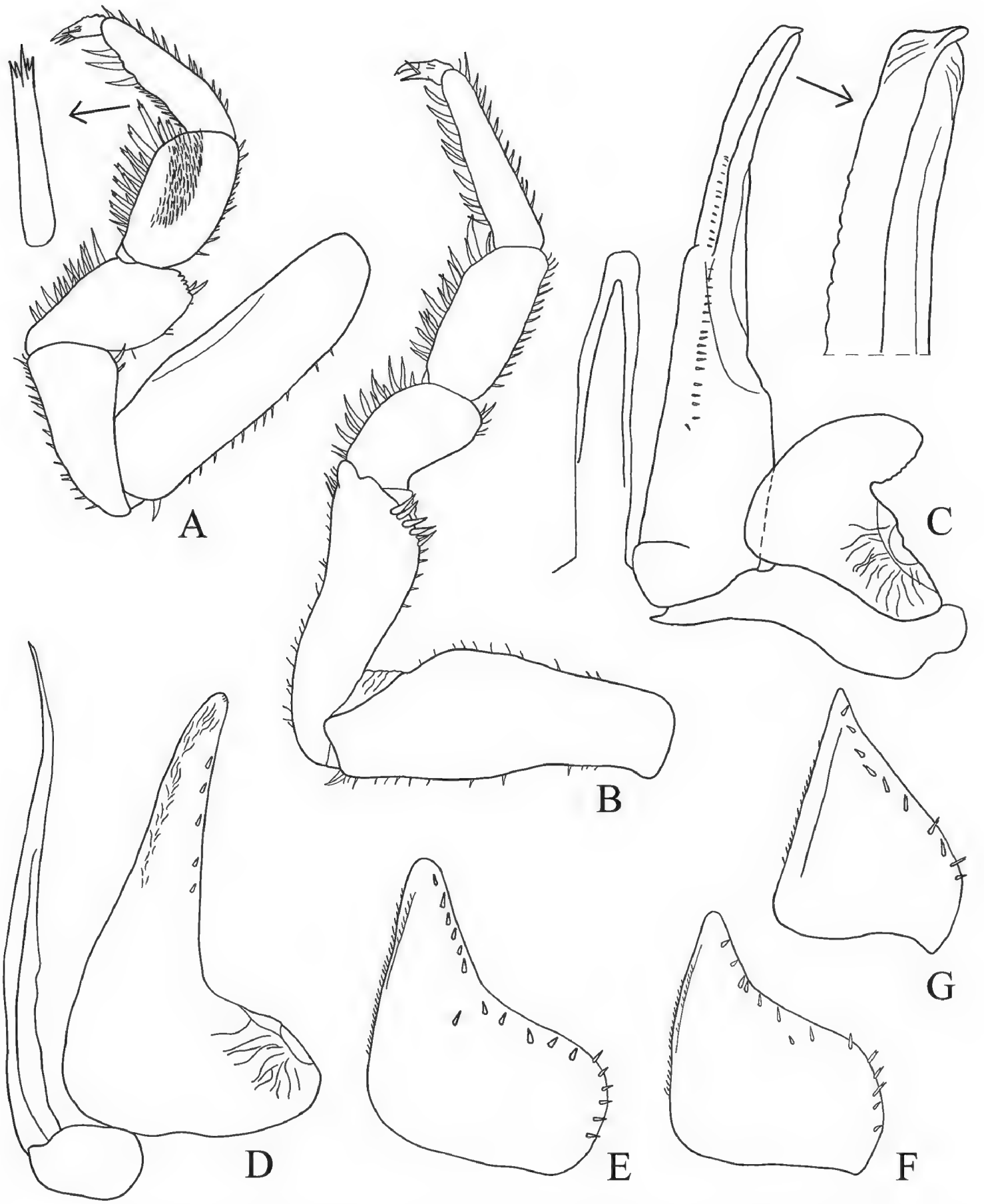

Figure 5. *Eluma cristata* sp. nov. Paratype ♂ from Alcobertas **A** pereopod 1 **B** pereopod 7 **C** genital papilla and pleopod 1 **D** pleopod 2 **E** pleopod 3 exopod **F** pleopod 4 exopod **G** pleopod 5 exopod.

shorter dorsal scale-setae of different shape (see fig. 4A–F in Cifuentes and Da Silva 2023).

Ecological notes. This species was only found in this MSS habitat.

Seasonal patterns in Portuguese MSS habitats. This species was only found in Alcobertas, during all seasons, and with a decrease in abundance from spring to summer, highest abundance during fall and a new decrease in winter (Fig. 7K).

Family Armadillidae Brandt, 1831
Genus *Armadillo* Latreille, 1802

***Armadillo officinalis* Duméril, 1816**
Fig. 6L

Armadillo officinalis Duméril, 1816: 117; Budde-Lund 1885: 16; Preudhomme de Borre 1886: 112; Dollfus 1896a: 357; Dollfus 1896b: 527; Arcangeli 1935a: 2; Vandel 1946: 371.
Cubaris globator; Eaton 1882: 361.
Cubaris officinalis; Jackson 1926: 184.

Material examined. Portugal – Arrábida • 28♂♂, 63♀♀; 38°28'59.2"N, 9°00'09.9"W; 21.VII.2022; leg. R.P. Eusébio; MSS pitfall trap; MNHNC:MB11:001139, 001153, 001156, 001168 • over 1000 individuals (♂ and ♀); 20.IX.2022; same data as for preceding; MNHNC:MB11:001232, 001239, 001241, 001244 • 84 ♂♂, 140 ♀♀, 2 juvs; 20.XII.2022; same data as for preceding; MNHNC:MB11:001305, 001309, 001312, 001318, 001321, 001331, 001334 • 1 ♀; 22.III.2023; same data as for preceding; MNHNC:MB11:001362.

Distribution. Widely distributed in the Mediterranean and Black Sea area.

Ecological notes. This epigean species can also be found in MSS.

Seasonal patterns in Portuguese MSS habitats. This species was only found in Arrábida, during all seasons, and abundance increasing from spring to summer where it reaches its peak, then decreasing in fall (Fig. 7L).

Ecological analysis

Terrestrial isopod communities differ across locations and seasons (Fig. 8). All species were found in either three or four of the sampled seasons (Fig. 7). The spatial distribution plot (Fig. 8A) shows that these communities are relatively different from each other among the five sampled locations. Serra da Estrela shows a distinctly different isopod community composition compared with other locations, largely driven by the strong influence of *Porcellio scaber* (Fig. 8A). Alcobertas also has a distinct community composition, characterized primarily by *Eluma cristata* and *Porcellio novus* (Fig. 8A). In contrast, the other three locations (Sicó, Arrábida, and Montejunto) show a greater overlap in species composition, suggesting more similar isopod communities (Fig. 8A).

The seasonal site-specific plots reveal varying degrees of variation in isopod communities (Figs 8B–F). In Serra da Estrela (Fig. 8B), isopod communities are composed only by two species with no clear seasonal pattern. In Sicó (Fig. 8C), Alcobertas (Fig. 8D) and Montejunto (Fig. 8E) the seasonal ellipses overlap almost completely, indicating similar isopod communities throughout the year in each location. In Arrábida (Fig. 8F) there is some demarked seasonal variation, with *Armadillo officinalis* and *Porcellionides cingendus* influencing summer and fall, and the other four species influencing spring.

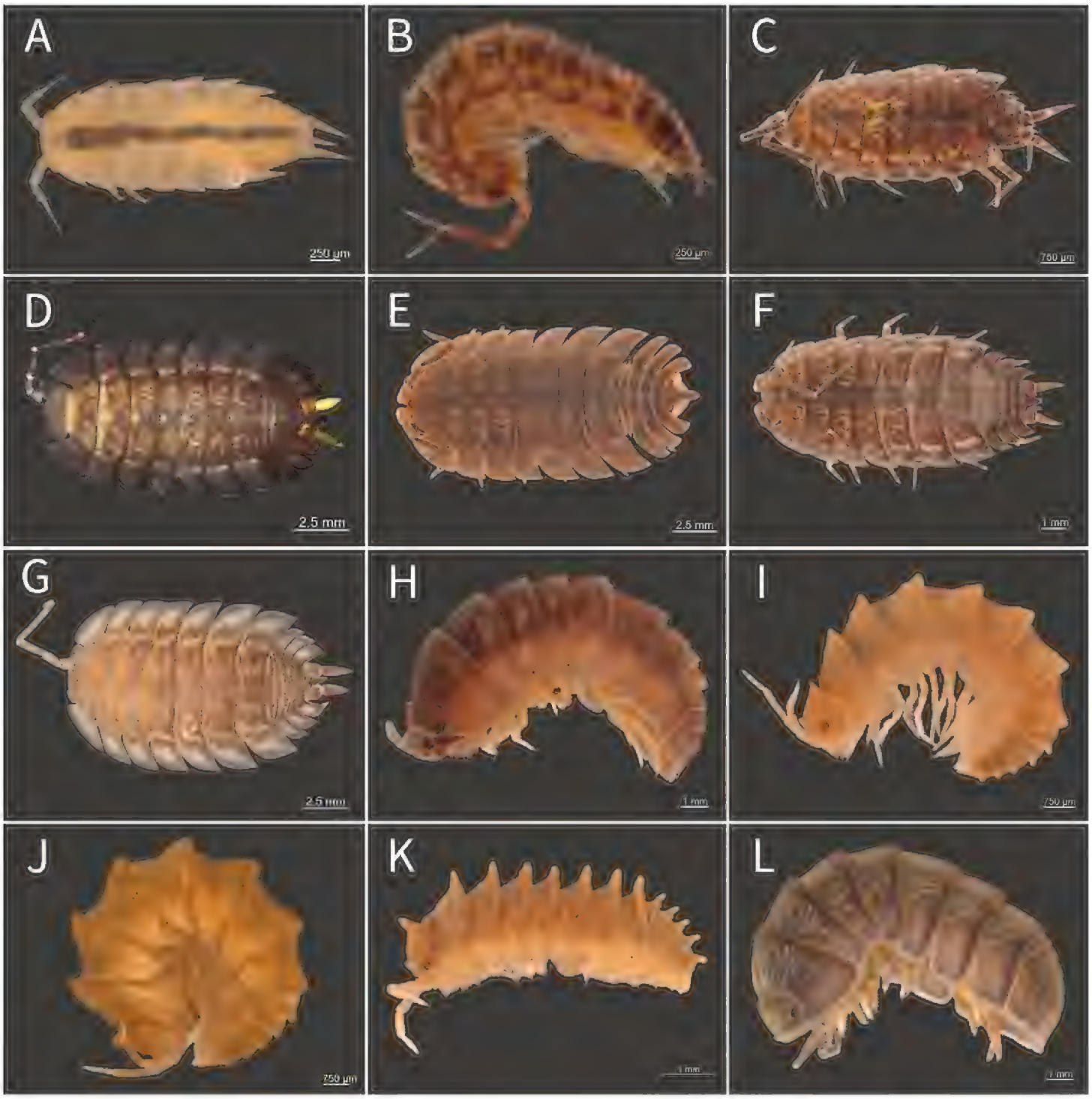

Figure 6. Specimen habitus **A** *Trichoniscoides machadoi* from Sicó **B** *Ctenoscia minima* from Montejunto **C** *Porcellionides cingendus* from Sicó **D** *Porcellio scaber* from Serra da Estrela **E** *Porcellio dilatatus* from Arrábida **F** *Porcellio dispar* from Sicó **G** *Porcellio novus* from Alcobertas **H** *Eluma caelata* from Montejunto **I** *Eluma tuberculata* from Sicó **J** *Eluma matae* from Montejunto **K** *Eluma cristata* sp. nov. from Alcobertas **L** *Armadillo officinalis* from Arrábida.

Discussion

We found 12 species of terrestrial isopods in Portuguese MSS habitats, belonging to five families, three more species and two more families than those recorded in a similar study done in Spain (Cifuentes et al. 2021). The most well represented family is Porcellionidae with five species, followed by Armadillidiidae with four, and the remaining families are only represented by one species each. This study revealed a new species, *Eluma cristata* sp. nov., found exclusively in the MSS of Alcobertas.

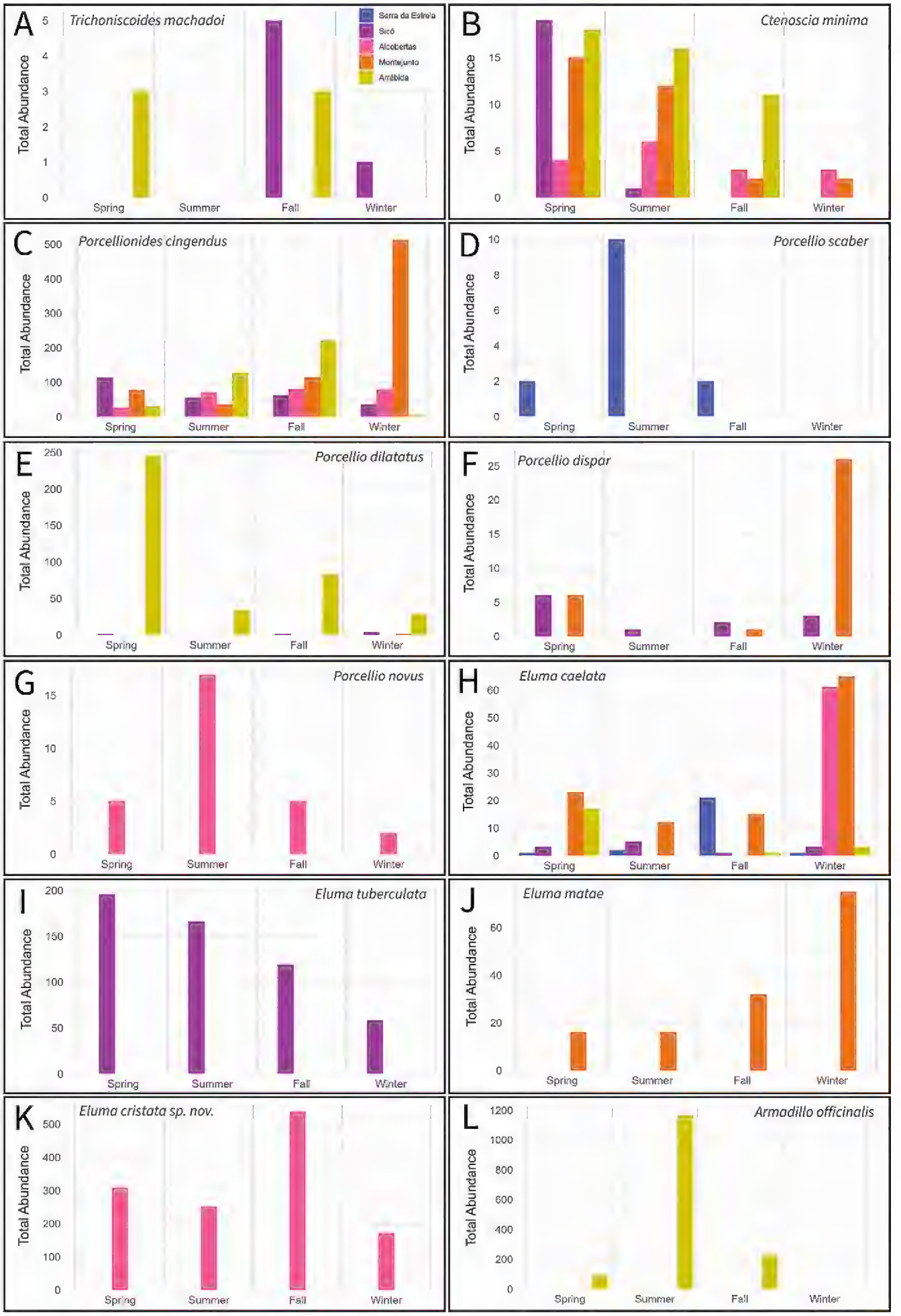

Figure 7. Total abundance per season for each of the species. Each colour represents one sampling location: blue – Serra da Estrela, purple – Sicó, pink – Alcobertas, orange – Montejunto, yellow – Arrábida **A** *Trichoniscoides machadoi* **B** *Ctenoscia minima* **C** *Porcellionides cingendus* **D** *Porcellio scaber* **E** *Porcellio dilatatus* **F** *Porcellio dispar* **G** *Porcellio novus* **H** *Eluma caelata* **I** *Eluma tuberculata* **J** *Eluma matae* **K** *Eluma cristata* sp. nov. **L** *Armadillo officinalis*.

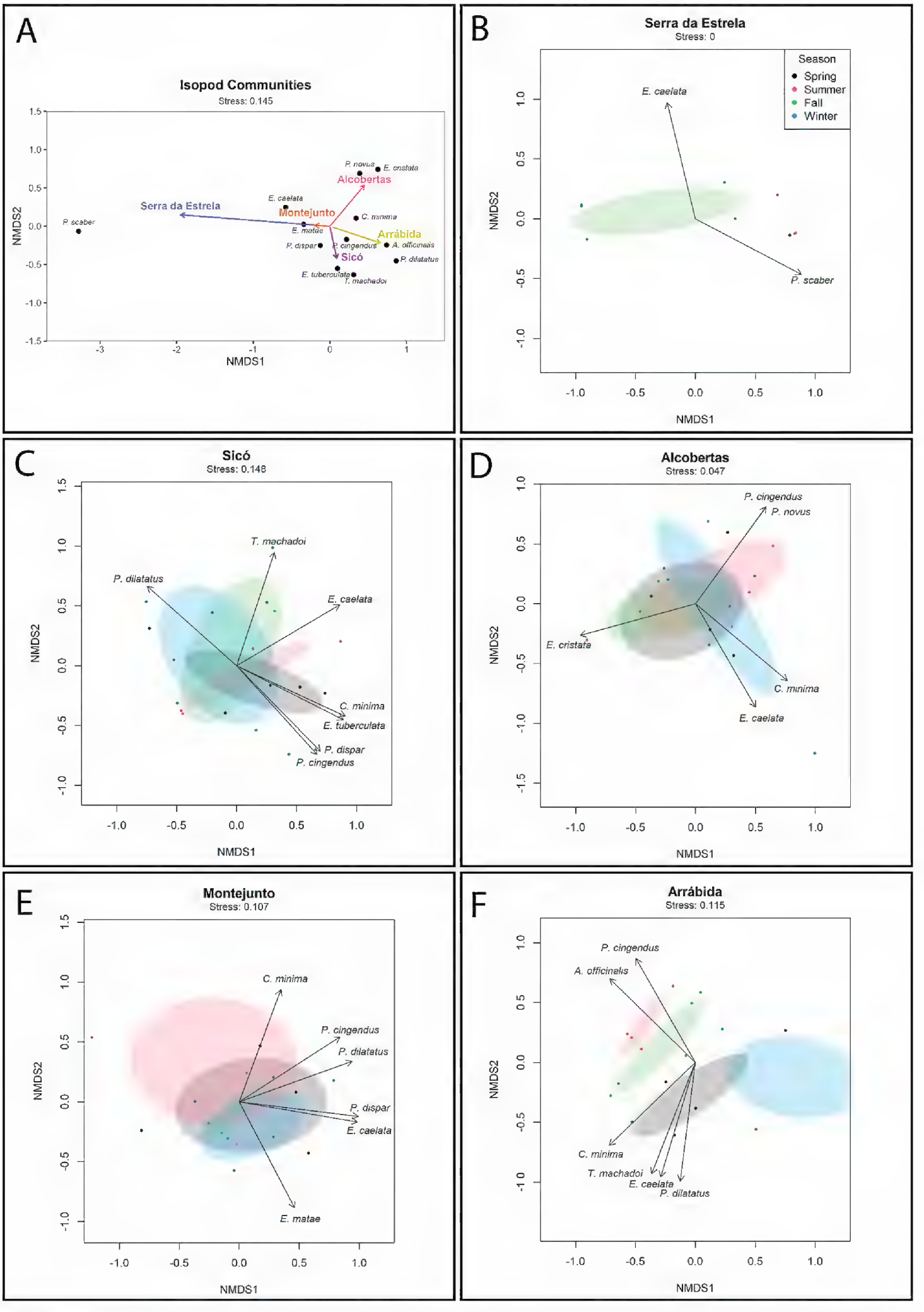

Figure 8. NMDS (Non-metric multidimensional scaling) of terrestrial isopod communities **A** species found in each of the five locations, with each point representing a species and each arrow representing a location **B–F** location specific seasonal NMDS **B** Serra da Estrela **C** Sicó **D** Alcobertas **E** Montejunto **F** Arrábida. In these panels each point represents one invertebrate trap (five traps per season), ellipses group the points by season, and the arrows represent the species.

The diversity of terrestrial isopods found in MSS habitats of Portugal includes both surface-dwelling species, such as *Ctenoscia minima*, *Porcellionides cingendus*, *Porcellio scaber*, *P. dispar*, *P. novus*, *Eluma caelata*, *E. matae*, and *Armadillo officinalis*, and species more frequently found in the surface-cave ecotone, such as *Trichoniscoides machadoi*, *Eluma tuberculata* and *Porcellio dilatatus* (Vandel 1946; Reboleira et al. 2015). This emphasises the connectivity between surface and subterranean habitats and reflects the broad ecological tolerance of terrestrial isopods and their preference for cryptic and dark environments (Hornung 2011; Dixie et al. 2015). On the other hand, the discovery of *Eluma cristata* sp. nov., highlights the relevance of shallow subterranean habitats as habitats for short range distributed species and high conservation value.

The spatial and seasonal distribution of terrestrial isopod species found in Portuguese MSS habitats displayed distinct patterns in abundance throughout the year. Widespread species such as *Ctenoscia minima* and *Porcellionides cingendus* were found in multiple locations and throughout all seasons, while *Eluma cristata* sp. nov. and *Porcellio novus* were restricted to single MSS sites. The use of MSS habitats by terrestrial isopod species differs depending on the location and species. Despite several species showing strong seasonal abundance patterns, seasonality does not seem to influence community composition in the majority of the studied locations.

Given the observed high diversity and ecological specialization, conservation of MSS habitats and their isopod communities is critical, not only in Portugal but worldwide. Despite being legally protected (ICNB 2000) and facing increasing threats (Mammola et al. 2019; Reboleira et al. 2022), MSS habitats and their fauna remain largely overlooked in biodiversity assessments. Therefore, their study and protection are essential to safeguard the unique invertebrate diversity they harbour.

Acknowledgments

This work was supported by the Portuguese National Funds through "Fundação para a Ciência e a Tecnologia" within the CE3C Unit funding (ref. UIDB/00329/2025), CHANGE (ref. LA/P/0121/2020) (https://doi.org/10.54499/LA/P/0121/2020) and PhD grant (ref. 2021.04868.BD) (https://doi.org/10.54499/2021.04868.BD), and by the Chair in Sustainability of Subterranean Ecosystems – Loulé, at the Faculty of Sciences of the University of Lisbon.

References

Arcangeli A (1935a) Gli isopodi terrestri del Portogallo. Bollettino del Laboratorio di Zoologia generale e agraria della RealeScuola superiore d'Agricoltura in Portici 29: 1–39.

Arcangeli A (1935b) Specie nuove di isopodi terrestri della Spagna raccolti dal Prof. F. Silvestri. Bollettino del Laboratorio di Zoologia generale e agraria del Regio Istituto superiore agrario in Portici 29: 40–46.

Arcangeli A (1948) Schizidiinae sottofamiglia di Armadillidiidae (crostacei isopodi terrestri). Bollettino dell'Istituto e Museo di Zoologia dell'Università di Torino 1: 211–272.

Brandt JF (1833) Conspectus Monographiae Crustaceorum Oniscodorum Latreillii. Bulletin de la Société impériale des Naturalistes de Moscou 6: 171–193.

Brandt JF, Ratzeburg JTC (1831) Isopoda. Gleichfüßler. In: Medizinische Zoologie oder getreue Darstellung und Beschreibung der Thiere, die in der Arzneimittellehre in Betracht kommen, in systematischer Folge herausgegeben. Trowitzsch und Sohn, Berlin 2: 70–84. [pls 12–13]

Budde-Lund G (1885) Crustacea Isopoda terrestria per familias et genera et species descripta. Nielsen and Lydiche, Copenhagen. https://doi.org/10.5962/bhl.title.109769

Cifuentes J (2019) Contribution à la connaissance des *Trichoniscoides* Sars, 1899 ibériques, avec la description de deux nouvelles espèces: *Trichoniscoides marinae* n. sp. et Tr. enoli n. sp (Crustacea, Isopoda, Trichoniscidae). Boletín de la Asociatión española de Entomologia 43(1–2): 27–54.

Cifuentes J, Da Silva LP (2023) The genus *Eluma* in the Iberian Peninsula, with the description of a new terrestrial isopod: *Eluma matae* sp. nov. (Oniscidea, Armadillidiidae, Eluminae). European Journal of Taxonomy 860: 27–41. https://doi.org/10.5852/ejt.2023.860.2047

Cifuentes J, Da Silva LP (2024) Revision of the genus *Porcellionides* Miers, 1877 (Isopoda: Porcellionidae) in the Ibero-Balearic region. European Journal of Taxonomy 939: 1–51. https://doi.org/10.5852/ejt.2024.939.2573

Cifuentes J, Martínez SL, Pardo JLM, Barranco P (2021) Isópodos (Crustacea, Oniscidea) del Medio Subterráneo Superficial (MSS) en el Sureste Ibérico (Almería, España). Boletín de la Asociatión española de Entomologia 45(3–4): 261–276.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18(1): 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Cruz A (1991) Especies nuevas o poco conocidas de isópodos terrestres de la Peninsula Ibérica. II. Isópodos epigeos de España y Portugal (Crustacea, Oniscidea). Bulletin de la Société d'Histoire naturelle de Toulouse 127: 71–75.

Culver DC, Pipan T (2009) The biology of caves and other subterranean habitats. Oxford University Press, New York. https://doi.org/10.1093/acprof:oso/9780199646173.001.0001

Culver DC, Pipan T (2014) Shallow subterranean habitats: ecology, evolution, and conservation. First edition. Oxford University Press, Oxford; New York.

Dixie B, White H, Hassall M (2015) Effects of microclimate on behavioural and life history traits of terrestrial isopods: Implications for responses to climate change. ZooKeys 515: 145–157. https://doi.org/10.3897/zookeys.515.9399

Dollfus A (1889a) Liste préliminaire des isopodes extramarins recueillis aux Açores pendant les campagnes de l'Hirondelle (1887–1888) par M. Jules de Guerne. Bulletin de la Société zoologique de France 14: 125–132.

Dollfus A (1889b) Isopodes terrestres recueillis aux Açores en 1887,1888 et 1889 par MM. Dr. Th. Barrois et le Lieutenant Chaves. Revue biologique du Nord de la France 1: 306–392.

Dollfus A (1892) Catalogue raisonné des isopodes terrestres de l'Espagne. Anales de la Sociedad española de Historia natural 21: 161–190.

Dollfus A (1896a) Sur la distribution géographique des Armadilliens en Europe. Compte-rendu des Séances du Troisième Congrès international de Zoologie Leyden, 1895, 356–358.

Dollfus A (1896b) Les isopodes terrestres du nord de l'Afrique, du Cap Blanc à Tripoli (Maroc, Algérie, Tunisie, Tripolitaine). Mémoires de la Société zoologique de France 9: 523–553.

Dollfus A (1897) Notes de géographie zoologique. Les Crustacés Isopodes terrestres a grande dispersion. La Feuille des Jeunes Naturalistes 27: 205–212.

Duméril A (1816) Armadille. Dictionnaire des Sciences naturelles 3: 115–117.

Eaton AE (1882) Note on *Rhacodes inscriptus*, Koch, and *Armadillo officinalis*, Duméril, terrestrial Isopoda. The Annals and Magazine of Natural History 10: 360–362. https://doi.org/10.1080/00222938209459726

Eusébio RP, Enghoff H, Solodovnikov A, Michelsen A, Barranco P, Salgado JM, Sendra A, Reboleira ASPS (2021) Temporal and spatial dynamics of arthropod groups in terrestrial subsurface habitats in central Portugal. Zoology 147: 125931. https://doi.org/10.1016/j.zool.2021.125931

Gregory SJ, Lee P, Read HJ, Richards P (2012) Woodlice (Isopoda: Oniscidea) collected from northwest Spain and northern Portugal in 2004 by the British Myriapod and Isopod Group. Bulletin of the British Myriapod and Isopod Group 26: 6–23.

Hornung E (2011) Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior. Terrestrial Arthropod Reviews 4: 95–130. https://doi.org/10.1163/187498311X576262

ICNB (2000) Plano Sectorial da Rede Natura 2000: Habitats Naturais (8130). https://www.icnf.pt/biodiversidade/natura2000/planosetorial

ICNF (2023) Livro Vermelho dos Invertebrados de Portugal Continental. https://lvinvertebrados.uac.pt/docs/Livro-Vermelho-dos-Invertebrados-de-Portugal-Continental.pdf

IUCN (2025) The IUCN Red List of Threatened Species. https://www.iucnredlist.org/en

Jackson HG (1926) Woodlice from Spain and Portugal, with an Account of *Benthana*, a Subgenus of *Philoscia*–Crustacea. Proceedings of the Zoological Society of London 96(1): 183–201. https://doi.org/10.1111/j.1096-3642.1926.tb01541.x

Jiménez-Valverde A, Gilgado ID, Sendra A, Pérez-Suárez G, Herrero-Borgoñón JJ, Ortuño VM (2015) Exceptional invertebrate diversity in a scree slope in Eastern Spain. Journal of Insect Conservation 19: 713–728. https://doi.org/10.1007/s10841-015-9794-1

Juberthie C, Delay D, Bouillon M (1980) Extension du milieu souterrain en zone non calcaire: description d'un nouveau milieu et de son peuplement par les Coléoptères troglobies. Mémoires de Biospéologie 8: 77–93.

Kinahan J (1857) Analysis of certain allied genera of terrestrial isopods; with description of a new genus, and a detailed list of the British species of *Ligia*, *Philougria*, *Philoscia*, *Porcellio*, *Oniscus* and *Armadillium* [sic]. Natural History Review 4: 258–282.

Koch L (1856) Crustacea. In: Rosenhauer WG. Die Thiere Andalusiens nach dem Resultate einer Reise zusammengestellt, nebst den Beschreibungen von 249 neuen oder bis jetzt noch unbeschriebenen Gattungen und Arten. Erlangen: Theodor Blaesing, 418–423.

Latreille PA (1804) Histoire naturelle, générale et particulière, des crustacés et des insectes. Cloportides 7: 25–49.

Mammola S, Amorim IR, Bichuette ME, Borges PAV, Cheeptham N, Cooper SJB, Culver DC, Deharveng L, Eme D, Ferreira RL, Fišer C, Fišer Ž, Fong DW, Griebler C, Jeffery WR, Jugovic J, Kowalko JE, Lilley TM, Malard F, Manenti R, Martínez A, Meierhofer MB, Niemiller ML, Northup DE, Pellegrini TG, Pipan T, Protas M, Reboleira ASPS, Venarsky MP, Wynne JJ, Zagmajster M, Cardoso P (2020) Fundamental research questions in subterranean biology. Biological Reviews 95(6): 1855–1872. https://doi.org/10.1111/brv.12642

Mammola S, Cardoso P, Culver DC, Deharveng L, Ferreira RL, Fišer C, Galassi DMP, Griebler C, Halse S, Humphreys WF, Isaia M, Malard F, Martinez A, Moldovan OT, Niemiller ML, Pavlek M, Reboleira ASPS, Souza-Silva M, Teeling EC, Wynne JJ, Zagmajster M (2019) Scientists' Warning on the Conservation of Subterranean Ecosystems. BioScience 69(8): 641–650. https://doi.org/10.1093/biosci/biz064

Mammola S, Giachino PM, Piano E, Jones A, Barberis M, Badino G, Isaia M (2016) Ecology and sampling techniques of an understudied subterranean habitat: the Milieu Souterrain Superficiel (MSS). The Science of Nature 103(11): 88. https://doi.org/10.1007/s00114-016-1413-9

Mammola S, Piano E, Giachino PM, Isaia M (2017) An ecological survey of the invertebrate community at the epigean/hypogean interface. Subterranean Biology 24: 27–52. https://doi.org/10.3897/subtbiol.24.21585

Miers EJ (1877) On a collection of Crustacea, Decapoda and Isopoda, chiefly from South America, with descriptions of new genera and species. Proceedings of the Zoological Society of London 1877: 653–679.

Nitzu E, Nae A, Giurginca A, Popa I (2010) Invertebrate communities from the mesovoid shallow substratum of the Carpatho-Euxinic area: eco-faunistic and zoogeographic analysis. Travaux de l'Institut Spéol."Émile Racovitza" 49: 41–79.

Nitzu E, Popa I, Giurginca A (2011) Invertebrate fauna (Coleoptera, Collembola, Diplopoda, Isopoda) collected in the karst areas of the Aninei-Locvei Mountains. Travaux de l'Institute de Spéologie "Émile Racovitza" 50: 15–35.

Nitzu E, Nae A, Băncilă R, Popa I, Giurginca A, Plăiaşu R (2014) Scree habitats: ecological function, species conservation and spatial-temporal variation in the arthropod community. Systematics and Biodiversity 12(1): 65–75. https://doi.org/10.1080/14772000.2013.878766

Norman A (1899) The land Isopoda of Madeira. Annals and Magazine of natural History (Series 7) 3: 66–70. [pl. 6] https://doi.org/10.1080/00222939908678078

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, Caceres MD, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette MH, Cunha ER, Smith T, Stier A, Braak CJFT, Weedon J, Borman T (2025) vegan: Community Ecology Package.

Preudhomme de Borre A (1886) Crustacés Isopodes recueillis par feu Camille Van Volxem, pendant son voyage en Portugal, en 1871. Comptes-Rendus des Séances de la Société entomologique de Belgique (Serie III) 72: 112–113.

R Core Team (2024) R: A language and environment for statistical computing (Version 4.4.2). R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reboleira ASPS, Eusébio RP (2021) Cave-adapted beetles from continental Portugal. Biodiversity Data Journal 9: e67426. https://doi.org/10.3897/BDJ.9.e67426

Reboleira ASPS, Eusébio RP (2023) Cave-adapted millipedes from Portugal: species conservation profiles. Biodiversity Data Journal 11: e110382. https://doi.org/10.3897/BDJ.11.e110382

Reboleira ASPS, Eusébio RP, Taiti S (2022) Species conservation profiles of cave-adapted terrestrial isopods from Portugal. Biodiversity Data Journal 10: e78796. https://doi.org/10.3897/BDJ.10.e78796

Reboleira ASPS, Goncalves F, Oromí P, Taiti S (2015) The cavernicolous Oniscidea (Crustacea: Isopoda) of Portugal. European Journal of Taxonomy 161: 1–61. https://doi.org/10.5852/ejt.2015.161

Recuero E, Rodríguez-Flores PC, García-París M (2022) Homoplasy and morphological stasis revealed through multilocus phylogeny of new myrmecophilous species in Armadillidiidae (Isopoda: Oniscidea). Zoological Journal of the Linnean Society 194(4): 1312–1340. https://doi.org/10.1093/zoolinnean/zlab066

Schmalfuss H (2003) World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttgarter Beiträge zur Naturkunde (Serie A) 654: 1–341.

Schmölzer K (1955) Landasseln aus Spanien, gesammelt von Prof. Dr. Ing. H. Franz. Ein Beitrag zur Kenntnis der Spanischen Isopodenfauna. Eos 31: 311–321.

Schmölzer K (1965) Ordnung Isopoda (Landasseln). Bestimmungsbücher zur Bodenfauna Europas, Issues 4 and 5. Academie Verlag, Berlin.

Schmölzer K (1971) Die Landisopoden der Iberischen Halbinsel. Monografías de Ciencia Moderna 80: 1–161.

Taiti S, Rossano C (2015) Terrestrial isopods from the Oued Laou basin, north-eastern Morocco (Crustacea: Oniscidea), with descriptions of two new genera and seven new species. Journal of Natural History 49(33–34): 2067–2138. https://doi.org/10.1080/00222933.2015.1009512

Vandel A (1946) Crustacés isopodes terrestres (Oniscoïdea) épigés et cavernicoles du Portugal. Anais da Faculdade de Ciências do Porto 30: 135–427.

Vandel A (1947) L'énigme de la reproduction des arthropodes cavernicoles et plus particulièrement des isopodes terrestres. Bulletin de la Société d'Histoire naturelle de Toulouse 82: 263–275.

Vandel A (1948) La faune isopodique française (Oniscoïdes ou Isopodes terrestres). Sa répartition, ses origines et son histoire. Revue française d'Entomologie 15: 101–139.

Vandel A (1952) Les trichoniscides (Crustacés – Isopodes) de l'hémisphère austral. Mémoires du Muséum national d'Histoire naturelle (Série A) 6: 1–116.

Verhoeff KW (1901) Über paläarktische Isopoden (7. Aufsatz). Zoologischer Anzeiger 24: 403–408, 417–421.

Verhoeff KW (1907) Über Isopoden, 10. Aufsatz. Zur Kenntnis der Porcellioniden. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin 8: 229–281.

Verhoeff KW (1908) Über Isopoden. 15. Aufsatz. Archiv für Biontologie 2: 335–387. [pls 29 –31]

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://doi.org/10.1007/978-3-319-24277-4_9